CHAPTER 4

Habitat related growth and reproductive investment in estuarine waters, illustrated for the tellinid bivalve *Macoma balthica* (L.) in the western Dutch Wadden Sea

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Abstract

In estuarine areas, bivalve species can be found in a variety of environments, where they experience large differences in environmental conditions. In the present paper, the importance of different habitats (intertidal, subtidal, adjacent coastal waters) for the persistence of the population was evaluated for the bivalve *Macoma balthica* (L.) in the western Dutch Wadden Sea estuary. Intra-specific variation in growth and reproductive output were followed during the year and related to local abiotic conditions. Significant differences in growth and reproductive investment were found between locations. Young individuals were mostly found in the intertidal area, where growth in terms of somatic mass was good. These areas were not favourable for adult individuals, since growth in shell length was low and many individuals did not reproduce. In the subtidal, where the highest densities were found, somatic and gonadal mass indices were low. Coastal areas had the lowest densities and showed high growth in terms of shell length and body mass. The habitat with the highest reproductive effort per individual was not the most important habitat in terms of reproductive output due to differences in density and in size of the habitat type. For *M. balthica*, the subtidal habitat contributed most to the reproductive output of the western Dutch Wadden Sea population although the highest reproductive output per individual was in the coastal area.

Introduction

Bivalve species can be found in a variety of environments, such as estuaries and coastal waters. In these areas, species experience differences in environmental conditions which influence their physiological processes. At a latitudinal scale, differences in growth rate of bivalves have been frequently related to latitudinal gradients in temperature (Gilbert 1973, Bachelet 1980, Appeldoorn 1983, 1995; Beukema and Meehan 1985, Hech et al. 2002, Fiori and Morsán 2004). However, at a local scale, other factors such as food quality and quantity, tidal level and sediment type seem to have a more important role (Newell and Hidu 1982, De Montaudouin 1996, Beukema and Cadée 1997, Honkoop and Beukema 1997, Beukema et al. 2002, Carmichael et al. 2004). An example is the observed higher growth, body condition and reproductive output in bivalves living at lower intertidal areas than at higher ones (Jones et al. 1978, Guevara and Niell 1989, Roseberry et al. 1991, Jensen 1992, Wanink and Zwarts 1993, De Montaudouin 1996, Honkoop and Beukema 1997), due to the longer submersion time and thus longer possibility of food intake at lower intertidal areas.

In the present paper, we aim to analyse intra-specific variation at a local scale for processes such as growth and reproduction. The tellinid bivalve *Macoma balthica* (L.) was selected for this study. *M. balthica* is a dominant species in many estuaries and coastal areas along the Atlantic coast (Dankers and Beukema 1983, Thompson and Nichols 1988, Harvey and Vincent 1989). *M. balthica* is a broadcast-spawning bivalve with separate sexes. After the release of gametes in the water column where fertilization occurs and a short planktonic larval period of about 3 to 4 weeks, larvae are ready to settle (Drent 2002). Initial settlement occurs mainly in the lower intertidal zone but during the summer animals migrate to the upper intertidal zone, where predation pressure of shrimps and crabs is relatively low (Armonies and Hellwig-Armonies 1992, Beukema 1993, Hiddink et al. 2002a). Before or during their first winter, spat migrates in the opposite direction and redistributes into deeper intertidal, subtidal and coastal waters (Beukema 1993). As a result, in Dutch waters, *M. balthica* is present in the intertidal and shallow subtidal areas in estuaries as well as in adjacent coastal waters (Beukema and De Bruin 1977, Dekker 1989).

The fact that *M. balthica* is widespread and common, illustrates a strong persistence of the population in these specific geographic spaces (c.f. Sinclair 1988), which would suggest favourable environmental conditions for the species. However, from an energetic point of view, at least the environmental conditions for the intertidal population hardly seem favourable, since for most of the year the energy balance is negative (Hummel 1985). During the summer, the high energy demand due to relatively high temperatures (Hummel 1985) and the suboptimal feeding conditions in the intertidal (only substantial food intake during submersion, Kamermans 1994), lead to weight and energy losses (Beukema and De Bruin 1977). Only during a relatively short period in spring, *M. balthica* is able to gain sufficient energy to compensate for these losses and even to grow and reproduce (Honkoop and Van der

Meer 1997). In subtidal and coastal areas, food conditions might be more suitable due to the fact that food intake is never hampered because of emersion. The fact that, during the summer, the decline in body condition is stronger at high intertidal levels than at low intertidal levels (Honkoop and Beukema 1997), suggests that at subtidal and coastal areas this difference may be even more marked. Whether spawning at the intertidal contributes substantially to recruitment is at present unclear and it cannot be excluded that the main contribution and hence persistence of the population originates from recruitment from the subtidal and/or coastal stocks.

Therefore, the final aim is to analyse the importance of the different habitats (intertidal, subtidal, coastal) for the persistence of the *M. balthica* population in the western Dutch Wadden Sea estuary. Growth and reproductive investment of *M. balthica* were analysed in the various habitats in order to test whether subtidal and coastal stocks are more important to the persistence of the population than intertidal ones. By analyzing age composition and following changes in somatic and gonadal mass in each habitat in relation to abiotic and biotic conditions, the energy investment into somatic and gonadal mass and, thus, the reproductive investment could be determined. In addition, the occurrence of gonad resorption during periods of unfavourable environmental conditions, as experimentally observed by Drent (2004) for this species, could also be studied by the analysis of seasonal patterns in gonadal mass.

Table 4.1. Characteristics of the locations sampled. Depth values are expressed as the difference between MTL and the mean intertidal level of each sampling site. Density ranges are shown between brackets.

Station	Latitude (ºN)	Longitude (ºE)	Depth (m)	Density (ind. m^{-2})
Intertidal	52° 55’	4° 48’	+0.1 – +0.3	74 (0 – 222)
Subtidal	53° 10’	5° 22’	-2.1 – -2.6	142 (17 – 167)
Offshore	52° 52’	4° 38’	-8 – -12	56 (5 – 75)

Materials and Methods

Field sampling

The sampling area was divided into three different habitat types based on water depth (Fig. 4.1, Table 4.1): the intertidal of the Wadden Sea, defined as the area above Low Low Water Spring (LLWS); the subtidal of the Wadden Sea (between LLWS and LLWS – 5 m); and the coastal zone of the North Sea (called here “offshore” and defined as the area between LLWS - 5 m and LLWS - 10 m).

Selection of sampling stations in the different habitats was based on information from long-term monitoring programmes. The sampling station in the intertidal was selected at the Balgzand, a large intertidal area which has been monitored since the 1970’s by Beukema and

co-workers (Beukema et al. 1978). The area between squares A and B of Beukema (1988, 1993) was selected because this area is considered to be representative for the intertidal in the western Wadden Sea (Beukema 1988, 1993; Beukema pers. comm.). At the subtidal, surveys in the western Wadden Sea have been carried out in 1982 and 1986. Densities of *M. balthica* were on average 42 ind. per m^2 in 1982 (Dekker 1989) and around 162 ind. per m^2 in 1986 (Van der Veer and Witte 1993, Van der Veer unpubl. data). An exploratory inventory in the largest subtidal area, Kimstergat, resulted in densities of *M. balthica* in line with previous numbers found in the subtidal in the western Wadden Sea (between 100 – 150 ind. m^{-2}) and therefore this large subtidal area was selected. In the offshore area, the distribution of *M. balthica* has been described by Daan and Mulder (2002, 2003, 2004) and Drent (2004). An exploratory inventory showed a similar distribution in recent years and the sampling area was selected within the areas sampled by these authors (Grote Keeten).

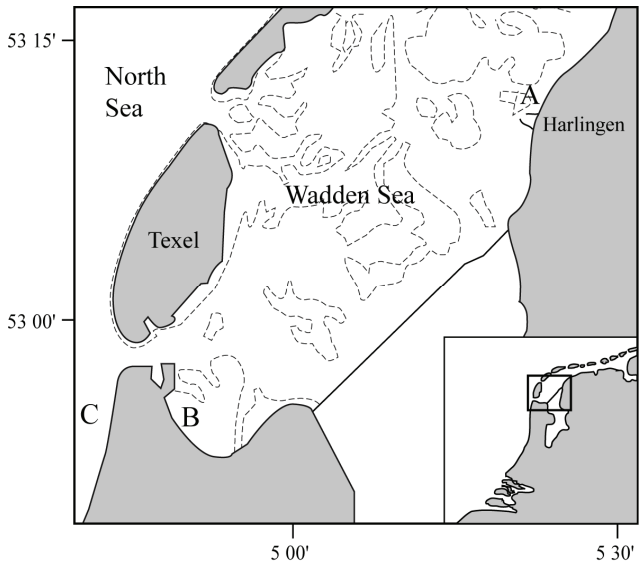

Fig. 4.1. Sampling locations of *M. balthica*: A) subtidal area; B) intertidal area and C) offshore area.

From September 2001 to April 2003, around 100 individuals were collected randomly in an area of a few km^2, if possible once a month. Intertidal samples were collected with hand cores (0.018 m^2) of approximately 30 cm deep during low tide. The intertidal site is submerged for an average of 5 h per tidal cycle. Subtidal samples were collected with a 'Reineck' box corer (0.06 m^2) during high tide. At the offshore station, due to low densities of a few animals per box corer, it was decided to sample with a 'Van Veen' grab (0.2 m^2). Previous research had shown that the distribution of *M. balthica* offshore is restricted to the first few cm in the sediment and that numbers caught by the grab were similar to those from the box corer, after correction for the differences in surface area (Beukema 1974). In the laboratory, all *M. balthica* were stored in seawater at 5 ºC and processed within the next 48 hours.

Data analysis

Of each individual *M. balthica*, shell length was measured to the nearest 0.01 mm with electronic callipers, and subsequently bivalves were opened and all flesh was removed. Animals that were parasitized with the trematode *Parvatrema affinis* (Swennen and Ching 1974) were discarded. Age was estimated by counting the shell's year marks (following Lammens 1967). Gonads were separated from body mass under a microscope and the ash-free dry mass (AFDM) of each part was determined to the nearest 0.01 mg, by drying for 4 days at 60 ºC and incinerating for 4 hours at 560 ºC. The difference between dry and ash mass represented the AFDM. For each individual, the condition index was determined by the Body Mass Index (BMI) as the total body AFDM mass (somatic mass + gonadal mass) divided by shell length^3. The investment in gonadal and somatic mass was determined by calculating the Somatic Mass Index (SMI) and the Gonadal Mass Index (GMI). SMI was defined as the AFDM of the soma divided by shell length^3 and GMI as the gonadal AFDM divided by shell length^3. The relative investment in reproduction was analysed by calculating the Gonadosomatic Ratio (GSR), expressed as the gonadal AFDM divided by the total body AFDM.

By dividing mass by cubic shell length, animals of different size could be compared in terms of mass. The extent to which variability in mass could be accounted for by seasonal variability and by differences among age classes and among locations was examined by using analysis of variance (ANOVA). Due to an unbalance in the sampling scheme over the year, the effect of time could not be described in terms of differences among all sampling months (that is, by using sampling month as a categorical variable). Instead we used a linear trend over time in combination with a sinusoidal seasonal effect. The overall time effect was, therefore, represented by:

$$\beta_1 \, Time + \beta_2 \sin(2\pi ((Month - \beta_3)/ 12)),$$

in which β_1, β_2, and β_3 are parameters, *Time* is a continuous variable that runs from the first day of observation till the last day, and *Month* is a continuous variable that runs from the first month of observation till the last month. Note that this model is only a linear model when β_3 is known beforehand. For that, we ran this linear model, which further included the factor site, for all 12 possible values of β_3 (i.e. the values 1 to 12) and selected the model with the lowest residual mean squares. Subsequently, the selected model was used to correct body, somatic and gonadal mass indices for seasonal and age differences, and adjusted to the average month and age. In order to obtain normality, only the GMI data needed to be transformed using the squared-root transformation.

In order to compare growth rates between populations, shell length (mm), somatic AFDM (mg) and gonadal AFDM (mg) were plotted against age. In order to avoid an underestimation

of maximum mass due to seasonal periods of decrease in mass, growth curves of somatic mass were estimated for the period of the year in which SMI was maximal. The Von Bertalanffy growth parameters were iteratively estimated and comparison between stations was made using the F-test. For that, non-linear regressions were run for all stations together, each station separately and for combinations of two stations. Multiple comparisons were done between the different regression models with the F-test.

Each sampling allowed an estimation of the instantaneous rate of annual decrease (M, y^{-1}), whereby constant mortality with age was assumed (i.e. exponential decrease in numbers). M was estimated by linear regression after ln transformation of the data, in which M corresponded with the slope of the regression. For that, the decrease in abundance from the age with the peak abundance to the oldest age was considered. This corresponded to individuals older than 0 years for the intertidal location, older than 2 years for the subtidal location and older than 4 years for the offshore location. Significant differences among locations were analysed using ANOVA and Fisher's LSD post-hoc test.

All statistical analyses were made using the software package SYSTAT (Wilkinson 1996).

Results

Age composition

The age composition of *M. balthica* differed between locations (Fig. 4.2). At the intertidal station individuals between 1 and 5 years old were present, with a high incidence of 1 year-old individuals. In the subtidal, most of the individuals were between 2 and 6 years old, with a maximum age of 11 years. In the offshore location, the largest age group consisted of 5 year old individuals and the maximum age was also 11 years, but relatively more individuals of 5 years were found compared to the subtidal location. After the summer, from July onwards, 0-group individuals were seen in the intertidal but not in the subtidal and offshore (Fig. 4.2).

The instantaneous rate of annual decrease (M) was 1.27±0.17 y^{-1} at the intertidal location, 0.39±0.16 y^{-1} at the subtidal location and 0.45±0.21 y^{-1} at the offshore location. This corresponded with an annual decrease of about 72% in the intertidal, 32% in subtidal and 36% offshore. Differences among locations were significant, due to significant differences between the intertidal and the subtidal/offshore locations (ANOVA, $F_{(2,31)} = 8.642$, $p = 0.001$). Between subtidal and offshore, M was not significantly different (Fisher's LSD post-hoc test, $p = 0.805$).

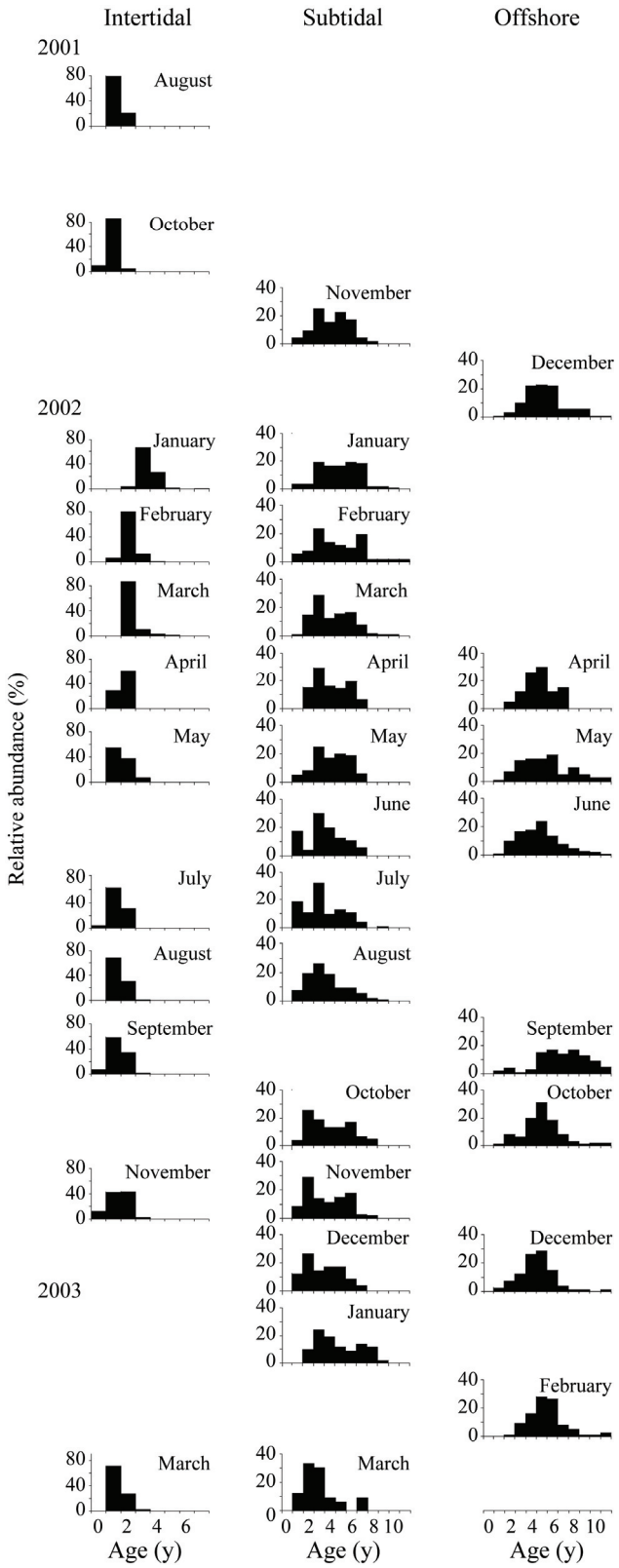

Fig. 4.2. Age composition (y) of intertidal, subtidal and offshore *M. balthica* populations for each sampling date between 2001 and 2003.

Growth

Maximum observed shell length was around 19 mm in the intertidal, 24 mm in the subtidal and 23 mm offshore (Fig. 4.3). Maximum values of somatic mass (mg AFDM) were around 90 mg for the intertidal, 120 mg for the subtidal and 130 mg offshore; and maximum gonadal mass (mg AFDM) was around 14, 28 and 35 mg for intertidal, subtidal and offshore respectively. The estimated maximum length was 15.7 mm for the intertidal, 21.7 mm for the subtidal and 21.0 mm for the offshore location (Table 4.2). Somatic mass-at-age curves were estimated for the month of May 2002 for the intertidal station and June 2002 for the subtidal and offshore stations (during which SMI was maximum, see next section).

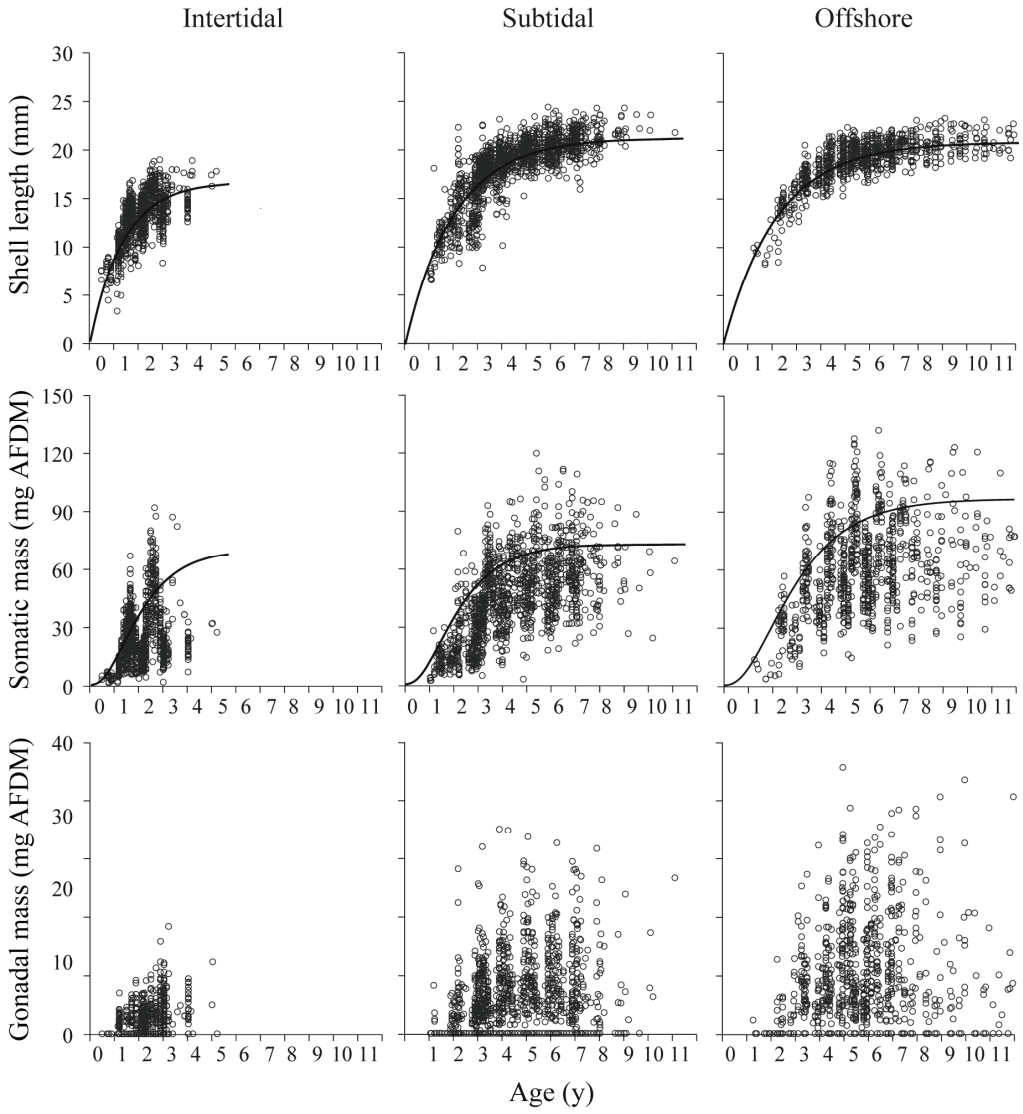

Fig. 4.3. Shell length (mm), somatic mass (mg AFDM) and gonadal mass (mg AFDM) of *M. balthica* plotted against age (y), with fitted Von Bertalanffy growth curves for shell length and somatic mass. The transition between two age groups is considered to be on the first of January.

The estimated maximum somatic mass was 69.4 mg for the intertidal, 72.1 mg for the subtidal and 96.2 mg for the offshore location. Since gonads are emptied during spawning, no growth curve was estimated. Statistically significant differences were found in shell length-at-age curves among locations (F-test, $F_{(2,3347)}$= 55.8, p<0.001), but not in somatic mass-at-age curves (F-test, $F_{(2,319)}$= 1.5, p>0.05). Overall, offshore individuals were the largest in terms of somatic mass and gonadal mass.

Table 4.2. Parameters of the Von Bertalanffy growth curve for maximum shell length (mm) and somatic mass (mg AFDW) of *M. balthica* at the three locations. L_∞ and W_∞ are the maximum asymptotic length (mm) and somatic mass (mg AFDM), k is the growth coefficient (d^{-1}), n is the number of individuals.

Parameter	Intertidal	Subtidal	Offshore
Length-at-age			
L_∞ (mm)	15.72	21.78	21.05
95% C.I.	15.39-16.06	21.56-22.04	20.87-21.23
k (*10^3; d^{-1})	2.503	1.286	1.255
95% C.I.	2.344-2.662	1.241-1.332	1.211-1.300
n	1077	1393	880
r^2	0.48	0.70	0.71
Somatic mass-at-age			
W_∞ (mg)	69.43	72.15	96.20
95% C.I.	51.65-90.94	66.18-78.46	90.64-101.98
k (*10^3; d^{-1})	2.191	2.015	1.525
95% C.I.	1.622- 2.760	1.682-2.348	1.363-1.687
n	48	97	177
r^2	0.58	0.65	0.53

Seasonal patterns in mass

Since no differences in body mass index (BMI), somatic mass index (SMI) and gonadal mass index (GMI) were found between males and females (ANOVA, p > 0.05), sexes were treated together in all analyses. Seasonal cycles of BMI were similar for the three locations (Fig. 4.4) with minimum values between January and March and maximum values around June. In the intertidal and offshore, the amplitude of values along the year was higher than in the subtidal. The latter also presented a lower BMI than the other two locations. BMI did not show much variation with age (Fig. 4.5), which was confirmed by the non-significance of the interaction term Station*Age (Table 4.3). Overall, significant differences in BMI were found between locations (Table 4.3), as reflected by the significant effects and interaction terms Station*Month and Station*Season. SMI had the same seasonal trend as the BMI (Fig. 4.4). The general linear model, showed significant differences in the interaction terms and in the

effects of month, season and age separately (Table 4.3). SMI was clearly lower in the subtidal than at the other two stations. Seasonal differences were smallest in the subtidal and strongest in the intertidal. SMI decreased significantly with age (Fig. 4.5) and this decrease was strongest in the intertidal.

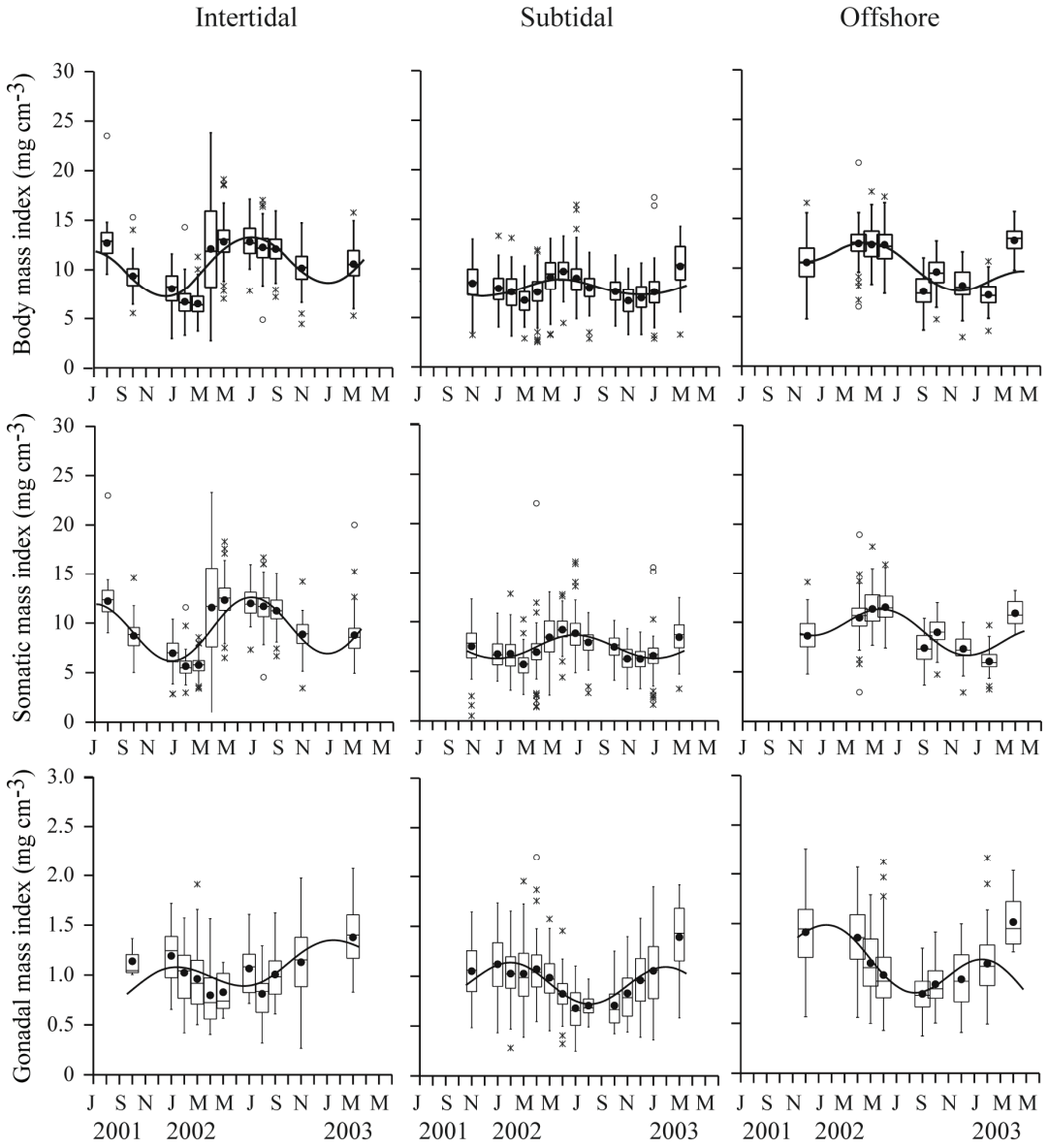

Fig. 4.4. Body mass index (mg cm^{-3}), somatic mass index (mg cm^{-3}) and gonadal mass index (mg cm^{-3}) of *M. balthica* along the year. Curves are model predictions. Data of gonadal mass index are square-root transformed. Full dots and horizontal bars indicate mean and median values, respectively; boxes represent the range within which the central 50% of the values fall; bars represent the data range excluding outliers; outliers and extreme values are, respectively, observations more than 1.5 and 3 times the box range and are represented by asterisks and open circles.

Cycles of GMI were similar for the three locations along the year, with higher values in January-March for 2002 and March-April for 2003 (Fig. 4.4). Lowest values of GMI were found in the months of August and September, during which the number of animals without any gonadal mass was higher (not shown). In the intertidal, this trend was not as obvious because many individuals were juveniles and did not reproduce. Overall, in the intertidal only 40% of the individuals sampled showed developed gonads, in contrast to 63 and 73% in the subtidal and offshore respectively (not shown).

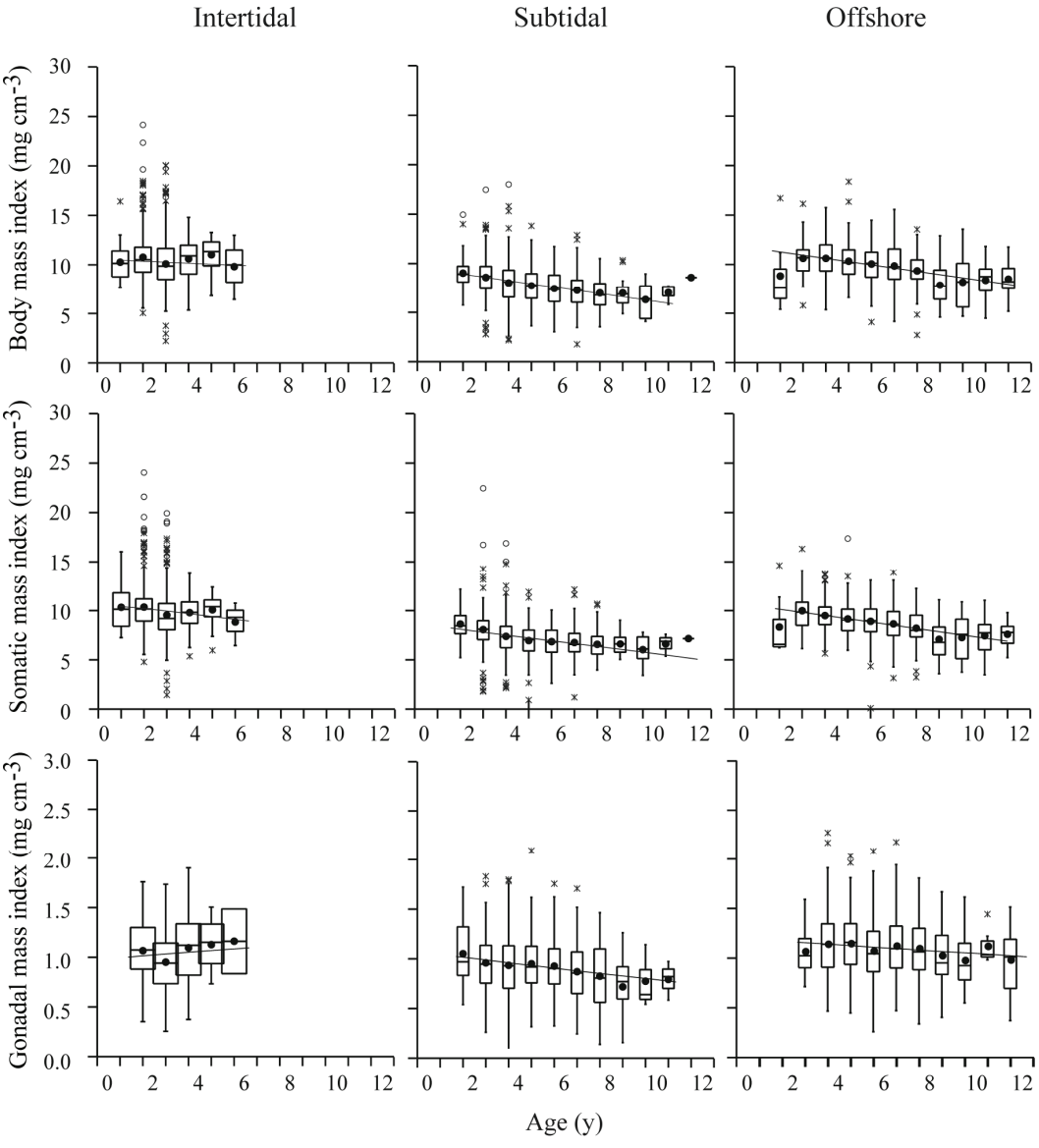

Fig. 4.5. Body mass index (mg cm-3), somatic mass index (mg cm-3) and gonadal mass index (mg cm-3) of *M. balthica* plotted against age (years) for the three stations. Lines are model predictions. Gonadal mass index data are square-root transformed. For more information see legend of Fig. 4.4.

On average, the highest GMI was found offshore. GMI showed significant differences between locations, but did not show a clear relation with age (Table 4.3, Fig. 4.5). In the three ANOVA tests done (for BMI, SMI and GMI), the residuals were normally distributed and there was no trend between residuals and estimates or time.

Table 4.3. Analysis of variance of the body, somatic and gonadal mass indices (mg cm^{-3}) of *M. balthica* from October 2001 to March 2003.

Source	Sum of Squares	df	Mean Square	F	p
Body Mass Index					
Station	979.979	2	489.990	109.795	<0.001
Month	100.925	1	100.925	22.615	<0.001
Season	4233.924	1	4233.924	948.726	<0.001
Age	197.324	1	197.324	44.216	<0.001
Station*Month	1126.317	2	563.158	126.191	<0.001
Station*Season	831.770	2	415.885	93.190	<0.001
Station*Age	17.693	2	8.847	1.982	0.138
Error	13477.501	3020	4.463		
Somatic Mass Index					
Station	673.169	2	336.585	74.113	<0.001
Month	240.548	1	240.548	52.967	<0.001
Season	546.045	1	546.045	120.235	<0.001
Age	2711.151	1	2711.151	596.974	<0.001
Station*Month	712.811	2	356.405	78.478	<0.001
Station*Season	416.902	2	208.451	45.899	<0.001
Station*Age	29.325	2	14.662	3.229	0.040
Error	14064.994	3097	4.541		
Gonadal Mass Index (SQRT-transformation)					
Station	7.693	2	3.847	41.962	<0.001
Month	0.408	1	0.408	4.450	0.035
Season	22.678	1	22.678	247.386	<0.001
Age	0.000	1	0.000	0.000	0.992
Station*Month	12.339	2	6.169	67.299	<0.001
Station*Season	1.622	2	0.811	8.847	0.001
Station*Age	0.722	2	0.361	3.938	0.020
Error	170.232	1857	0.092		

From the decline of GMI in 2002, the spawning periods for the different locations were estimated. In the intertidal, gonadal mass decreased in January-February. In the subtidal and offshore, the decrease occurred later in the season, around April-May (Fig. 4.4). In 2003, sampling stopped before a drop in gonadal mass occurred. The timing of spawning appeared

to be earlier for the intertidal (around February) and at lower water temperature (7-8 °C, Cardoso pers. obs.) than at the subtidal and offshore locations (spawning around May at a water temperature of about 11 °C, Cardoso pers. obs.). Gonadosomatic ratio (GSR) was similar between locations (Fig. 4.6). However, in 2002, a clear difference in peaks in GSR could be seen, with highest values in the offshore location and lowest in the intertidal one. Offshore, about 20% of the total body mass consisted of gonads, in contrast with 15% in the subtidal and 10% in the intertidal.

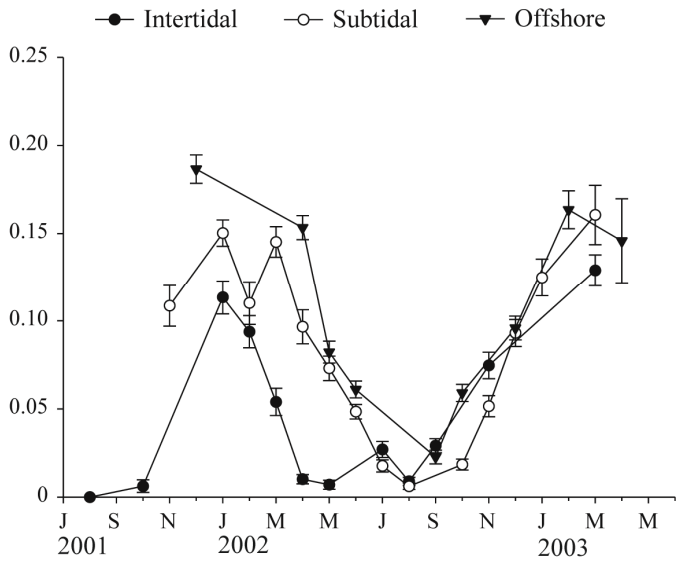

Fig. 4.6. Gonadosomatic ratio (-) of *M. balthica* throughout the year at each location.

To analyse the importance of the different habitats for the persistence of the *M. balthica* population in the western Dutch Wadden, the contribution in terms of gonadal mass (g AFDM m^{-2}) was determined for each habitat in 2002 and 2003. First, the mean gonadal mass per individual was estimated for each age group before spawning (in 2002 for the months of February for intertidal and subtidal locations and December for offshore; in 2003 in the months of March for intertidal and subtidal and April for offshore). Next, a weighted mean gonadal mass per individual (g AFDM ind^{-1}) for the whole population (all age groups) was calculated. Finally, the mean gonadal mass per individual for each area was converted in contribution per m^2 by multiplying with the average density per m^2 (see table 4.1). Results are presented in Table 4.4.

Table 4.4. Estimated contribution in terms of gonadal mass (g AFDM m^{-2}) of each habitat.

Station	Weighted mean gonadal mass (g AFDM ind^{-1})	Contribution per m^2 (g AFDM m^{-2})
2002		
Intertidal	4.3	316.9
Subtidal	9.4	1336.0
Offshore	15.5	868.5
2003		
Intertidal	2.1	159.0
Subtidal	6.3	888.3
Offshore	13.9	778.3

Discussion

Population structure in relation to habitat

Age determination was done by counting the external winter growth marks, a method validated by Lammens (1967). However, in old individuals (> 6 years old) growth marks are closer to each other and more difficult to visualize. Also the earlier rings tend to become less visible (Lammens 1967). This may partially explain some of the observed variability in individual growth within each location. Nevertheless, clear differences in age composition between intertidal and subtidal/offshore locations, illustrate that different life stages prefer different habitats. In this study, 0 years-old *M. balthica* were only found in the intertidal location and not in the subtidal and offshore, confirming that, in general, spat is concentrated in the intertidal (Günther 1991, Beukema 1993, Hiddink and Wolff 2002). This is in agreement with studies on migration patterns of *M. balthica* in the Wadden Sea, reporting settlement in intertidal areas and redistribution to lower intertidal and subtidal areas during the first year of life (Beukema and De Vlas 1989, Beukema 1993, Hiddink and Wolff 2002). The factor triggering initial settlement is unknown.

No individuals older than 5 years were observed in the intertidal, possibly reflecting higher adult mortality in these areas than in subtidal and offshore areas. During submersion, predation by shrimps, crabs and polychaetes (Van der Veer et al. 1998, Hiddink et al. 2002a, Hiddink et al. 2002b) will mainly affect young individuals. In addition, during emersion, adults suffer from predation by birds (Hulscher 1982, Zwarts and Blomert 1992, Dekinga and Piersma 1993). Under the assumption that adult migration is insignificant, the higher instantaneous rate of decrease in the intertidal, might suggest that bird predation is the main factor behind differences in density of adult individuals between habitats. In subtidal and offshore areas, *M. balthica* is not exposed to this type of predation but the existence of predation by large crabs cannot be excluded (Hiddink et al. 2002a).

In bivalves, growth is indeterminate and the asymptotic maximum size is habitat dependent (Sebens 1987). Food availability and other environmental factors affect the physiological costs and influence maximum size. With respect to abiotic conditions, water temperature is by far the most important rate controlling factor. Both the annual temperature patterns as well as mean weekly temperatures were roughly similar for the three locations (Cardoso pers. obs.; http://www.nioz.nl; http://www.waterstaat.nl).

When comparing shell growth between different populations along a latitudinal gradient (Beukema and Meehan 1985, Drent 2004), *M. balthica* from the Wadden Sea showed higher growth than populations from northern and southern locations. This suggests that differences in food conditions between locations may be more important than temperature differences. In other bivalve species, such as scallops (MacDonald and Thompson 1985a, Bricelj et al. 1987, MacDonald and Bourne 1987, Navarro et al. 2000), mussels (Bayne and Worrall 1980, Page and Hubbard 1987, Borrero 1987) and oysters (Paterson et al. 2003), growth rates also seemed to be mainly controlled by food availability. In this respect, feeding conditions for growth of *M. balthica* seem more favourable in the subtidal and offshore: growth of shell is higher at these continuously submerged locations than at the intertidal, also when only similar age classes are considered. Better feeding conditions could be the result of the higher percentage of silt in the water in the subtidal than in the intertidal (Dekker and Waasdorp 2004, Dekker et al. 2002, 2003), leading to higher sedimentation and a potential for better food supply. However, this can not be accessed by the data presented in the present study.

Seasonal patterns in relation to habitat

The seasonal trends in body mass index (BMI), somatic mass index (SMI), and gonadal mass index (GMI) in the intertidal were in accordance with previously described patterns for the Balgzand area (Beukema 1974b, Zwarts 1991, Honkoop and Beukema 1997, Drent 2004). In the subtidal and offshore, these indices followed a similar trend. However, the seasonal variation was different, probably due to differences in food conditions between areas, which could not be accessed by this study. In the intertidal and offshore, the decline in SMI is stronger than in the subtidal, suggesting that either energy uptake is lower or maintenance costs are higher at these locations. In the intertidal, extremely high temperatures during the summer may lead to higher maintenance costs than in the subtidal and offshore locations.

Despite the higher shell growth in the subtidal location than in the intertidal one, GMI is the lowest in the subtidal suggesting poor feeding conditions in this area. In other bivalve species, low food availability has been related to reduced reproductive output (MacDonald and Thompson 1985b, Bayne et al. 1983, MacDonald et al. 1987, Delgado and Camacho 2003). In addition, in *M. balthica*, gonadal development occurs at the expense of body (and somatic mass), since body mass declines with the increase in gonadal mass (De Wilde 1975, Nichols and Thompson 1982, this study). Such patterns have also been observed in other species (MacDonald and Thompson 1986, Lodeiros and Himmelman 1999, Delgado and

Camacho 2003). In this study, the subtidal area had the lowest growth in somatic and gonadal mass.

Importance of different habitats

Selection for higher reproductive output should result in a lower life-span (Calow 1979) and our results seem to support this idea. If subtidal and offshore locations are compared, on average higher reproductive output is observed offshore, but asymptotic size is higher in the subtidal. This evidence is stronger if different latitudinal populations of *M. balthica* are compared (Drent 2004). In comparison to Wadden Sea *M. balthica* populations, populations from Balsfjord (Norway) showed higher reproductive output (about 35% of gonad in relation to total body mass during the peak in gonadosomatic ratio in the Balsfjord vs. 15% in the Wadden Sea) but lower asymptotic length (about 16 mm in the Balsfjord vs. 21 mm in the Wadden Sea). Similar patterns of reduced life-span with increased reproductive output were observed in populations of scallop *Placopecten magellanicus* along its distributional limits in the northwest Atlantic (MacDonald and Thompson 1988).

Intertidal areas are especially important for a relatively short period in the life cycle of *M. balthica,* when spat settles and grows during the first years of life. Although *M. balthica* becomes mature and reproduces at the intertidal, the low percentage of adults with developed gonads and the negative energy balance for most of the year suggest that the contribution in terms of reproductive output might be restricted. The fact that growth and body condition of adults is low in the intertidal, and that most of the individuals do not reach sexual maturation clearly indicates these areas are mainly nursery areas and not good areas for growth and reproduction of adult individuals, at least for *M. balthica*. The subtidal area, with high densities of animals, has the lowest body condition, with low somatic and gonadal mass indices while the offshore location, with the lowest density, shows high BMI, SMI and GMI. Although SMI is similar between intertidal and offshore locations, the main difference lays on the amount of gonads, which is higher offshore. Taking in account that the GMI is low in the subtidal and that somatic and reproductive growth conditions for adult *M. balthica* are not favourable in the intertidal, the amount of spat produced per individual must be higher at the offshore location.

In the western Dutch Wadden Sea, the intertidal, subtidal and offshore areas correspond to about 500 km^2, 1200 km^2 and 450 km^2, respectively (Beukema 1989, Dekker 1989, Holtmann et al. 1996). Inside the Wadden Sea, in intertidal and subtidal areas, densities of *M. balthica* have shown strong variability in the last two decades. In the beginning of the eighties, the contribution of *M. balthica* in terms of total biomass production was higher in the intertidal (Dekker 1989). However, in more recent studies, biomass production was clearly higher in the subtidal areas (Dekker et al. 2002, 2003; Dekker and Waasdorp 2004). Comparing the different habitats and years in terms of contribution in gonadal mass per m^2 (g AFDM m^{-2}), resulted in a ratio of 1:4:3 for intertidal, subtidal and offshore, respectively, in 2002 and in a

ratio of 1:6:5 for intertidal, subtidal and offshore in 2003. For an estimation of the total gonadal mass per habitat, the gonadal mass (g AFDM m^{-2}) was multiplied by the area of each habitat (see above), resulting in a ratio of 1:10:2 for the intertidal, subtidal and offshore habitats in 2002 and 1:13:4 for the intertidal, subtidal and offshore habitats in 2003. Despite the fact that offshore animals present higher body condition and higher reproductive output, it is the subtidal area that contributes with most reproductive output in terms of biomass, due to the high densities of *M. balthica* found in these areas. It should be kept in mind that these values are only an indication of the order of magnitude since variability in BMI, SMI and GMI within each habitat was not accounted for. Furthermore, strong year-to-year variability in densities will influence the contribution of each area. These aspects should be part of a future study.

Acknowledgments: We thank the crews of RV 'Navicula' and RV ‘Stern’ for assistance during sampling. Jan Beukema, Wim Wolff, Jaap van der Meer, Jan Drent, Oscar Bos, Pieter Honkoop, Katja Philippart, Pauline Kamermans and two anonymous reviewers provided critical comments on earlier drafts of the paper.

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